A *SPORANGIOSTROBUS* WITH *DENSOSPORITES* MICROSPORES

by W. G. CHALONER

ABSTRACT. A new lycopod cone, *Sporangiostrobus ohioensis* sp. nov., is described from the Pennsylvanian of Ohio, U.S.A. It contains megaspores similar to *Superbisporites superbus* (Bartlett) Potonié and Kremp, and microspores agreeing with *Densosporites solaris* Balme. The genus *Densosporites* Berry *sensu* Potonié and Kremp is now known to represent at least two distinct groups of lycopods, and this offers a basis for a natural subdivision of the genus. An emended diagnosis of *Sporangiostrobus* is given.

THE extensive work of the last thirty years on Carboniferous spores constitutes an important source of potential palaeobotanical information. The correlation of such dispersed spores with their parent plants both enhances the intrinsic palaeobotanical interest and status of the isolated spores themselves, and also throws light on aspects of the contemporaneous flora which may not be apparent from the study of the compression fossils alone. This paper is an account of the remains of a large lycopod cone containing megaspores and microspores of Pennsylvanian age from Ohio, U.S.A. The significance of the cone lies mainly in its establishing the source plant of the miospore *Densosporites solaris* Balme and confirming the hermaphrodite nature of the genus *Sporangiostrobus*. It is also only the second specimen of this cone genus to be found in North America. The ubiquitous occurrence of the genus *Densosporites* in Carboniferous spore assemblages, and the association of certain species of the genus with coals of a durainous character has added particular interest to its source-plants.

I must express my grateful thanks to the Director of the New York Botanical Garden and to Dr. H. Becker, through whose kindness I was able to borrow the specimen on which this paper is based.

Source and nature of the material and method of investigation. The specimen described here as *Sporangiostrobus ohioensis* sp. nov. is in the Palaeobotanical Collection of the New York Botanical Garden, and carries a printed label with the name of J. S. Newberry and the locality 'Cuyahoga Falls, Ohio'. The cone or cone fragments are in the form of compressions consisting of little more than the spore contents of sporangia still arranged in the position that they occupied in the cone (text-fig. 2; Plate 10, fig. 5), on black, highly carbonaceous shale. The only other macrofossils present are numerous fragments of Cordaite leaves and possibly some Pteridosperm rachises. Dr. J. M. Schopf (personal communication, Oct. 1959) says of the locality, Cuyahoga Falls, 'in the old collections, material from the same horizon above the Sharon Coal in this neighbourhood is likely to be labelled either Akron, Tallmadge or Cuyahoga Falls. From . . . [the photograph of the holotype] I would guess that this specimen is on the Sharon Roof Shale.' Moore *et al.* 1944 (Correlation chart 6) show the Sharon in the New River Group of the Pottsville Series, a horizon equivalent to the lower part of the Westphalian A of the European sequence.

The megaspores in the cone were visible to the naked eye (Plate 10, fig. 5; text-fig. 2)

[Palaeontology, Vol. 5, Part 1, 1962, pp. 73–85; pls. 10–11.]

and could easily be removed with a mounted needle. They were then macerated in Schulze's solution (nitric acid saturated with potassium chlorate) for a few hours and transferred to dilute ammonia. This removed the adhering coaly matter, but the spores were still opaque bodies which could be examined only by reflected light. Some of these spores were then placed in concentrated nitric acid until they became transparent (the time required varied between individual spores, but did not exceed six hours), the spores were then removed into distilled water, and from that directly into absolute alcohol. After dehydration these spores were mounted in Canada balsam for examination by transmitted light (Plate 11, fig. 7). The description of the megaspores is based on both these transparent preparations and the less macerated, opaque spores which were mounted dry in air cells.

The microspores were prepared by macerating small fragments from individual microsporangia in Schulze's solution; after treating a sporangial fragment for six hours it was removed from the solution and transferred to a weak ammonia solution. In this the fragment was teased apart, the excess liquid drawn off with filter paper, and the remaining spores and spore aggregates mounted in glycerine jelly containing saffranin. Several slides were made from different sporangia, representing collectively many thousands of spores.

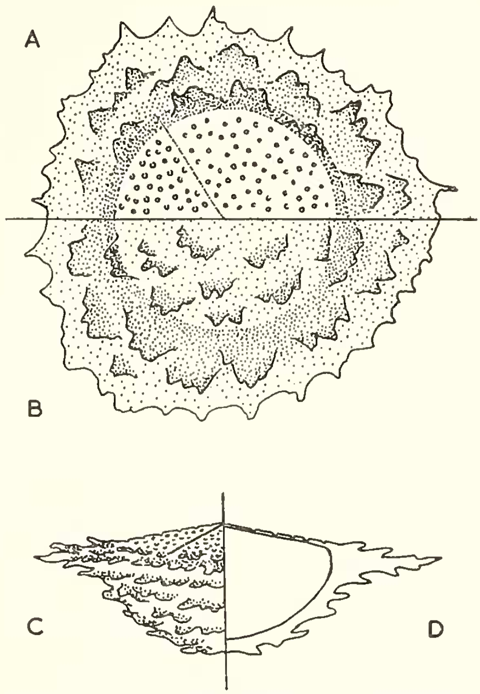
DESCRIPTION

The cone. The cone itself (Plate 10, fig. 5; text-fig. 2) consists of two aggregates of sporangia, in a more or less orderly arrangement suggesting that they were originally part of a single cone which had become broken into two short segments during fossilization. The cone was clearly hermaphrodite; the megasporangia can be seen to contain megaspores with the naked eye, while the microsporangia look smooth. Although there are groups of megasporangia and microsporangia they do not appear to be aggregated into well-defined zones as in some of the arborescent lycopod cones.

The megasporangia appear to have contained only one (or possibly in some cases, two) tetrads of megaspores. The microsporangia must have contained several thousands of microspores.

The microspores. The microspores are triradiate, subtriangular to nearly circular in outline in polar view, as seen in preparations from the cone (Plate 10, figs. 1–4; text-fig. 1). Originally the proximal face must have been more or less pyramidal, and the distal more or less hemispherical, before fossilization. The mean maximum diameter of fifty spores is 55 μ (range 42–70 μ, standard deviation 5·6 μ). The triradiate mark can occasionally be seen (Plate 10, fig. 2) as three fine radiating lines extending to the margin of the body, but not to the margin of the equatorial feature. The spore is thickened in the region of the equator to form a projecting flange which becomes thinner away from the spore body until at the margin it is membranous; the flange *s.l.* must therefore have been more or less wedge-shaped in section. In this it shares some of the characters of both a 'cingulum' and a 'zona' *sensu* Potonié and Kremp 1955; I refer to it as a cingulum. Measured from the spore cavity or lumen to the outer margin, the cingulum forms one-quarter to one-fifth of the total spore diameter, as seen in polar view. The distal face of the spore is covered with more or less conical processes of varied size (typically 2–5 μ high) which may be partially fused at their bases, in twos or threes, forming groups or cristae aligned more or less parallel to the equator (text-fig. 1; Plate 10; figs. 1–4). These coni and cristae extend all over the distal face and on to both surfaces of the cingulum, but not on to the contact faces; the latter are almost smooth, but show an L–O pattern (? due to fine micropunctate sculpture). The membranous margin of the cingulum is irregularly serrate, individual serrations being typically 1–3 μ (exceptionally 6 μ) long, and of varied width.

The spores obtained from the cone show no greater degree of variation in size or morphology than 'populations' of spores obtained from other comparable fossil lycopod cones (Chaloner 1958*a*, *b*, Bhardwaj 1958). Only a single spore was seen which showed almost total absence (? obliteration) of the sculpture; this was attributed to overmaceration rather than state of maturity, on the basis of Bhardwaj's (1958) convincing demonstration of the effect of overmaceration in his *Porostrobus* spores. Aside from this single spore, no variation comparable to Bhardwaj's was obtained, but no attempt was made to induce it by deliberate overmaceration.



TEXT-FIG. 1. A reconstruction of a microspore of *Sporangiostrobus ohioensis* sp. nov., × 1,000. Above, in polar view, below, in equatorial view. A, Proximal face. B, Distal face. C, External surface. D, Imaginary median section.

Evidently, in both a coal and in spore masses obtained from a fossil cone, spores towards the outside of a fragment will receive more maceration than those inside, and in any generally satisfactory maceration there may always be some spores which have become overmacerated. Bhardwaj's study has been particularly valuable in showing the effect that such overmaceration can induce in what was apparently a rather uniform population of a single cone. The recent demonstration by Potonié and Schweitzer (1960) of a high degree of innate variation in the contents of a fossil fructification makes it important to discriminate between the types of variation that can be produced by overmaceration (such as that of Bhardwaj) and normal phenotypic and/or ontogenetic variation within a fossil spore population (such as that of Potonié and Schweitzer).

The species of dispersed spore, nearest to the microspores obtained from *Sporangiostrobus ohioensis*, is *Densosporites solaris* Balme (1952). Samples of the spores from the cone were sent to Dr. A. H. V. Smith (Sheffield), Dr. M. A. Butterworth (Chester), Professor R. Potonié and Dr. H. Grebe (Krefeld) who agreed independently (personal communications, 1959) that this is the closest species to the spores in the cone. Balme gave the size of his species as 39–65 μ (mean 49 μ), somewhat smaller than that of the measured population of *S. ohioensis* microspores. The range of *D. solaris* is Westphalian A to C; Potonié and Kremp 1956*a* give A to B, but Butterworth and Millott (1960) record it also in the Westphalian C. A further species of dispersed spore, *Densosporites indignabundus* (Loose) S.W. and B. (= *Cristatisporites indignabundus* (Loose) P. and K. 1954) is very similar to those obtained in the cone. Balme acknowledged the similarity of this species to his *D. solaris* saying that '*D. solaris* . . . resembles an extreme variant of the species *D. indignabundus*.' The latter species was nevertheless subsequently made the type species of a new genus, *Cristatisporites*, Potonié and Kremp 1954. It can fairly be said that the genus *Cristatisporites* is very similar to several of the species included in *Densosporites*, and that the delimitation of these two genera is not very satisfactory.

When they first erected the genus *Cristatisporites*, Potonié and Kremp (1954) did not regard it as having a cingulum or equatorial thickening, but merely as being characterized by cristate sculpturing. Bhardwaj (1957) subsequently reinterpreted *Cristatisporites* as having 'a thickened peripheral region comparable in structure and organization to the cingulum of *Densosporites* and *Lycospora*'. Potonié (1958, p. 27) subsequently accepted this interpretation.

A number of other species similar in varying degrees to those present in *Sporangiostrobus ohioensis* sp. nov. have been described occurring as dispersed spores. Unfortunately some authors do not always indicate how their new species differ from previously described ones. The following species appear to be significantly similar to those obtained from the cone, and are cited to illustrate the considerable number of species placed either in *Densosporites* or *Cristatisporites* which are not strikingly different from those here described. Their stratigraphic range and the values for the maximum diameter are given. The range of the latter values may show either the mean (in brackets) or the value for the holotype or figured specimen (in italics):

Denso-sporites pannosus Knox 1950, p. 326, pl. 18, fig. 267 (Namurian), 62 μ.
Denso-sporites type A, Hoffmeister *et al.* 1955, p. 387, pl. 36, fig. 20 (High Dinantian), *54* μ.
Denso-sporites spinifer Hoffmeister *et al.* 1955, p. 386, pl. 36, figs. 16, 17 (High Dinantian), 32–(46)–48 μ.
Cristatisporites indignabundus (Loose) Potonié and Kremp 1955 (who give a complete synonymy), p. 105, pl. 16, figs. 294–5 (Westphalian B–C), 50–*52*–80 μ.
Cristatisporites connexus Potonié and Kremp 1955, p. 106, pl. 16, figs. 291–3 (Westphalian B), 45–*56*–70 μ.
Densosporites duriti Potonié and Kremp 1956*a*, p. 117, pl. 18, figs. 383–4 (Westphalian B), 45–(68)–70 μ.
Cristatisporites splendidus Artüz 1957, p. 247, pl. 4, fig. 22 (Westphalian A), 45–(55)–63 μ.
Densosporites belliatus Artüz 1957, p. 252, pl. 6, fig. 43 (Westphalian A), 40–(43)–55 μ.
Cristatisporites cf. *indignabundus* (Loose) P. and K., Bhardwaj 1957, p. 105, pl. 27, figs. 31–32 (? Westphalian C), 40–55 μ.
Cristatisporites elegans Bhardwaj 1957, p. 105, pl. 27, figs. 29, 30 (? Westphalian C), 38–(44)–48 μ.
'*Densosporites decorus* (Loose)' Dybova and Jachowicz 1957, p. 163, pl. 48, figs. 1–4 (Westphalian B–D), *55* μ. (This is apparently a later homonym of *Cristatisporites indignabundus* (Loose) P. and K., the holotype of which is included in Dybova and Jachowicz's synonyms.)
Densosporites spinosus Dybova and Jachowicz 1957, p. 164, pl. 49, figs. 1–4 (Namurian A–Westphalian B), *48* μ.
Densosporites verrucosus Dybova and Jachowicz 1957, p. 166, pl. 50, figs. 1–4 (Namurian A–Westphalian C), 32–*50*–54 μ. (This is apparently a later homonym of *Densosporites glandulosus* Kosanke, the holotype of which is included in Dybova and Jachowicz's synonyms.)
Densosporites cf. *indignabundus* Alpern 1958, figs. 8, 26, and 27 (Stephanian), 56–60 μ.
Densosporites cf. *indignabundus* Alpern 1959, pl. 8, figs. 210–14 (Stephanian), 50–80 μ.

Microspores indistinguishable from those in *S. ohioensis* (i.e. *Densosporites solaris*

Balme) have therefore been recorded from the Westphalian A–C, and rather similar spores (i.e. those listed above) from the Dinantian to the Stephanian.

The microspores that Bode (1928) obtained from his *Sporangiostrobus rugosus* were described as having a rough, warty surface and a diameter of 70–90 μ. Some apparently showed a triradiate mark. Although these spores were evidently larger than those obtained from *S. ohioensis* this description and the photographs are not otherwise inconsistent with Bode's spores (of *S. rugosus*) having been similar to *Densosporites solaris*. Nemejc's microspores of *S. feistmanteli* (1931, unnumbered plate, figs. 5–8) had a 'densely mamillous' surface, a size-range of about 40–50 μ, and his photographs suggest a thickened equatorial feature. To this extent they seem even more closely comparable with *D. solaris*.

In addition to the microspores yielded by macerating the microsporangia of *S. ohioensis*, several fragments of cuticle were obtained, showing the outline of oblong polygonal cells. These cuticle fragments lacked stomata or other distinctive features, and in this and other respects were similar to those figured by Bode (1928) and Nemejc (1931) from their cones. These authors suggested that the cuticles represent sporangial walls; unless the character of the sporangia was very different from that of *Lepidostrobus*, for example (with very thick-walled prismatic wall cells, isodiametric in surface view), this seems unlikely. It is at least equally probable that these cuticle fragments are the remains of the cuticle of the basal part of the sporophyll lamina, or even of that part of the sporophyll to which the sporangium was attached.

The megaspores. The megaspores obtained from *Sporangiostrobus ohioensis* sp. nov. are large, triradiate, and must originally have had a more or less pyramidal proximal face, a hemispherical distal face, and a broad flange attached to the equator (Plate 11, fig. 7). The spore body outline is round to subtriangular, 1,800–2,200 μ (mean 2,042 μ, standard deviation 116 μ for 19 measured). The mean wall thickness is typically 60 μ. The greatest observed width of the equatorial flange is 560 μ, at one of the radial extremities of the triradiate mark, and rather less in the inter-radial sectors. The equatorial feature was evidently the most vulnerable part of the spore, and had frequently been damaged in removing the megaspores from the cone. Its width, intact, could therefore only be measured on a few specimens, and mean measurements are of little value in these circumstances. The triradiate mark extends to the equator, the lips are tall (up to 550 μ), strongly undulating, and diminishing slightly in height from the extremities towards the pole. The contact faces are ornamented with sparsely distributed rounded tubercles about 15 μ in all dimensions, and occasional conical spines, 10–15 μ wide at the base and up to 50 μ long. The distal face of the spore is ornamented with a dense covering of hairs (Plate 11, fig. 5), of more or less cylindrical shape, with a rounded, blunt or somewhat swollen apex. These are rather more sparse, or even absent, at the centre of the distal face, but they remain fairly uniform over the remainder, only becoming markedly denser in the immediate equatorial region where they merge into the equatorial flange. This is composed of numerous more or less flattened bifurcating and anastomosing processes which merge together at their bases (Plate 11, figs. 3, 7). Adjacent processes are sometimes partially connected by a membrane of spore-coat substance to produce a flange varying in texture between a loose reticulum with actual gaps, to a more or less continuous fluted membrane. The processes comprising the flange commonly have rather stronger cross-connexions at the periphery than nearer to the spore body (sometimes giving individual processes a hammer-headed appearance) so that 'windows' in the equatorial feature are commonest in the outer third of its width, and are more abundant than actual breaks in the margin of the flange. This equatorial feature or flange therefore has some of the characters of both a zona and a corona (*sensu* Potonié and Kremp 1955).

The spores found in the cone may be compared in the most general terms with three genera of dispersed megaspores:

1. *Superbisporites* Potonié and Kremp 1954. (Type: *S. superbus* (Bartlett) P. and K.)
2. *Zonalesporites* (Ibrahim) Potonié and Kremp 1954. (Type: *Z. brasserti* (Stach and Zerndt) P. and K.)
3. *Rotatisporites* Potonié and Kremp 1954. (Type: *R. rotatus* (Bartlett) P. and K.)

These three genera have in common a broad zonal (equatorial) feature, and they are separated from one another mainly on the character of this feature. Dijkstra (1952, 1956), Dijkstra and Pierart (1957), Dijkstra and Van Vierssen Trip (1946), Potonié and Kremp (1956*a*), and Winslow (1959) discuss these dispersed spores fully. Broadly speaking, *Superbisporites* is the largest and has a more or less continuous equatorial feature of closely woven hairs which may show gaps (or 'windows') near the periphery (see Plate 11, figs. 1, 2). The hairs forming this feature may continue as much shorter bristles all over the distal face of the spore. *Zonalesporites* is similar but smaller, the equatorial feature or flange is normally continuous, uninterrupted by breaks or 'windows', and ends abruptly on the distal face of the spore which is more or less smooth. *Rotatisporites* has an equatorial feature which differs (at least in the type species) from either of the other two genera in having a more or less continuous rim supported by more or less discrete spokes, like a cart-wheel (Plate 11, fig. 4). However, one species assigned to this genus, *R. ramosus* (Arnold) (Plate 11, fig. 6), shows a less pronounced version of this rim-with-spokes structure, making it rather closer to *Superbisporites*.

The distinctions between these three genera are in some cases rather hard to maintain. Kalibova (1950), for example, was unable to discriminate between the type species of *Zonalesporites* and *Superbisporites*, and treated the two together as a single taxon. Similarly, *Triletes dentatus* Zerndt has been placed in *Superbisporites* by Potonié and Kremp (1956*a*), while Dijkstra (1952, p. 167) says that 'no essential points of difference can be observed between this species and *T. ramosus* Arnold 1950' which Potonié and Kremp (1956*a*) place in the genus *Rotatisporites*. While this does not, of course, constitute in itself a case for regarding these three genera as synonyms, it does emphasize the rather trivial nature of the features on which they have been separated.

The megaspores of *Sporangiostrobus ohioensis* undoubtedly show closest agreement with *Superbisporites superbus* (Bartlett) P. and K. in size, the character of the triradiate mark, the distal appendages and the general aspect of the equatorial flange, but differ from it in having a rather less continuous structure to this feature (cf. Plate 11, figs. 3 and 7 with figs. 1 and 2). In this respect, only, do they show some similarity to *Rotatisporites ramosus* (Arnold) P. and K. (Plate 11, fig. 6). In the structure of the equatorial flange, the megaspores of *Sporangiostrobus ohioensis* might be said to be intermediate between *Superbisporites superbus* (with a more or less continuous flange of anastomosing processes) and *Rotatisporites ramosus* (with a more clearly defined 'rim with spokes' structure).

SYSTEMATIC DESCRIPTION

Genus SPORANGIOSTROBUS Bode 1928, emend.

Type species. S. feistmanteli (O. Feistmantel) Nemejc 1931.

Emended diagnosis. Large lycopod cone, consisting of a massive axis occupying more than half the total cone diameter, bearing spirally arranged sporophylls. Sporangia apparently either axillary or borne on the upper surface of the sporophyll, the distal part of which extends as a long linear lamina. Cone hermaphrodite (? or bearing either megaspores or microspores). Megaspores triradiate, large (greater than 1,000 μ), bearing a broad equatorial flange formed of fused and anastomosing hairs. Microspores triradiate with an equatorial thickening which tapers to a thin marginal flange (cingulum).

Discussion. The genus *Sporangiostrobus* was first described by Bode (1928) who described two species based on large microspore-bearing cones, lacking sporophyll laminae, from Silesia. He suggested that the cones belonged either to the Pteridophytes or Pteridosperms. Nemejc (1931) compared Bode's cones with some Czech specimens, from one of which he was able to extract both megaspores and microspores, and accordingly reinterpreted Bode's genus as a heterosporous lycopod fructification; he compared *Sporangiostrobus* with other arborescent lycopod cones, particularly *Sigillariostrobus* (for discussion of the distinctions between *Sporangiostrobus*, *Polysporia*, *Lepidostrobus* and *Sigillariostrobus* see Chaloner 1958*a*). It now seems appropriate to formally emend Bode's original diagnosis of the genus *Sporangiostrobus*, this emendation being based both on the material described by Nemejc and that discussed here. It is largely influenced by Nemejc's interpretation of the cone, but this is now strengthened by the knowledge that at least two specimens were hermaphrodite, and by evidence as to the real nature of the microspores.

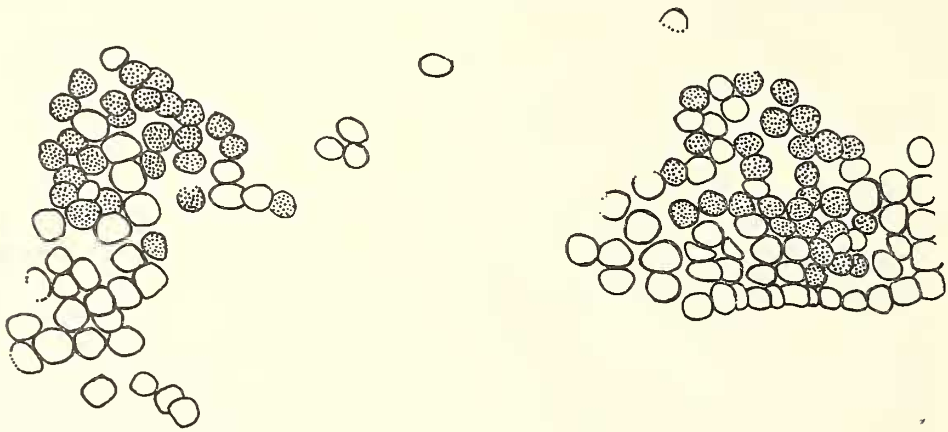
Sporangiostrobus ohioensis sp. nov.

Plate 10, figs. 1–5; Plate 11, figs. 3, 5, 7

Diagnosis. Cone cylindrical, at least 4 cm. in diameter and in length, probably considerably longer. Sporophylls spirally arranged, exposed (outer) ends of the sporangia more or less polygonal, 4 mm. in height and width. Megasporangia and microsporangia more or less segregated into several zones, each megasporangium containing a single megaspore tetrad, and each microsporangium containing several thousand microspores. Megaspores large (central body up to 2,200 μ), triradiate, and with a broad equatorial flange (up to 550 μ wide) of partially fused hairs forming a more or less continuous feature with occasional gaps towards the periphery; hairs forming the flange occupying a relatively narrow equatorial region, merging rapidly away from the equator into short, more or less cylindrical hairs which cover the whole distal spore surface. Microspores triradiate, mean diameter 55 μ with an equatorial thickening, extending for about one-fifth the total diameter, which diminishes in thickness away from the spore body to a thin membrane at the margin. Distal spore surface covered with conical spines, adjacent spines being partially fused at their bases to form cristae more or less parallel to the equator; these extend on to the equatorial feature, which has a serrate margin; proximal spore surface minutely punctate.

Holotype. Specimen No. 8134G, Palaeobotanical Collection of the New York Botanical Garden, New York, U.S.A.

Locality. Cuyahoga Falls, near Akron, Ohio. From approximately the horizon of the Sharon Coal, probably the roof shale of that seam; New River Group, Pottsville Series (approximately the equivalent of the lower part of the Westphalian A of Europe).



TEXT-FIG. 2. Drawing of the cone segments of *Sporangiostrobus ohioensis* sp. nov. holotype, ×1, showing the arrangement of the megasporangia (stippled) and microsporangia (plain). Cf. Plate 10, fig. 5.

GENERAL DISCUSSION

Other species of Sporangiostrobus. The following species of *Sporangiostrobus* have already been described:

1. *Sporangiostrobus feistmanteli* (Feistmantel) Nemejc 1931, hermaphrodite and megaspore-bearing; Upper Carboniferous from several localities in Czechoslovakia (Nemejc, loc. cit.) and Limburg, Holland (Jongmans 1936). Bode (1928, p. 247) cited '? *Sigillariostrobus Feistmanteli*' under *Sporangiostrobus* but did not specify it as the type species of his genus. Nemejc (1931, p. 72) first made the combination '*Sigillariostrobus* (*Sporangiostrobus* Bode) *Feistmanteli*' so that *S. feistmanteli* must be attributed to him; I agree with Jongmans (1936) that *S. feistmanteli* should be regarded as the type species

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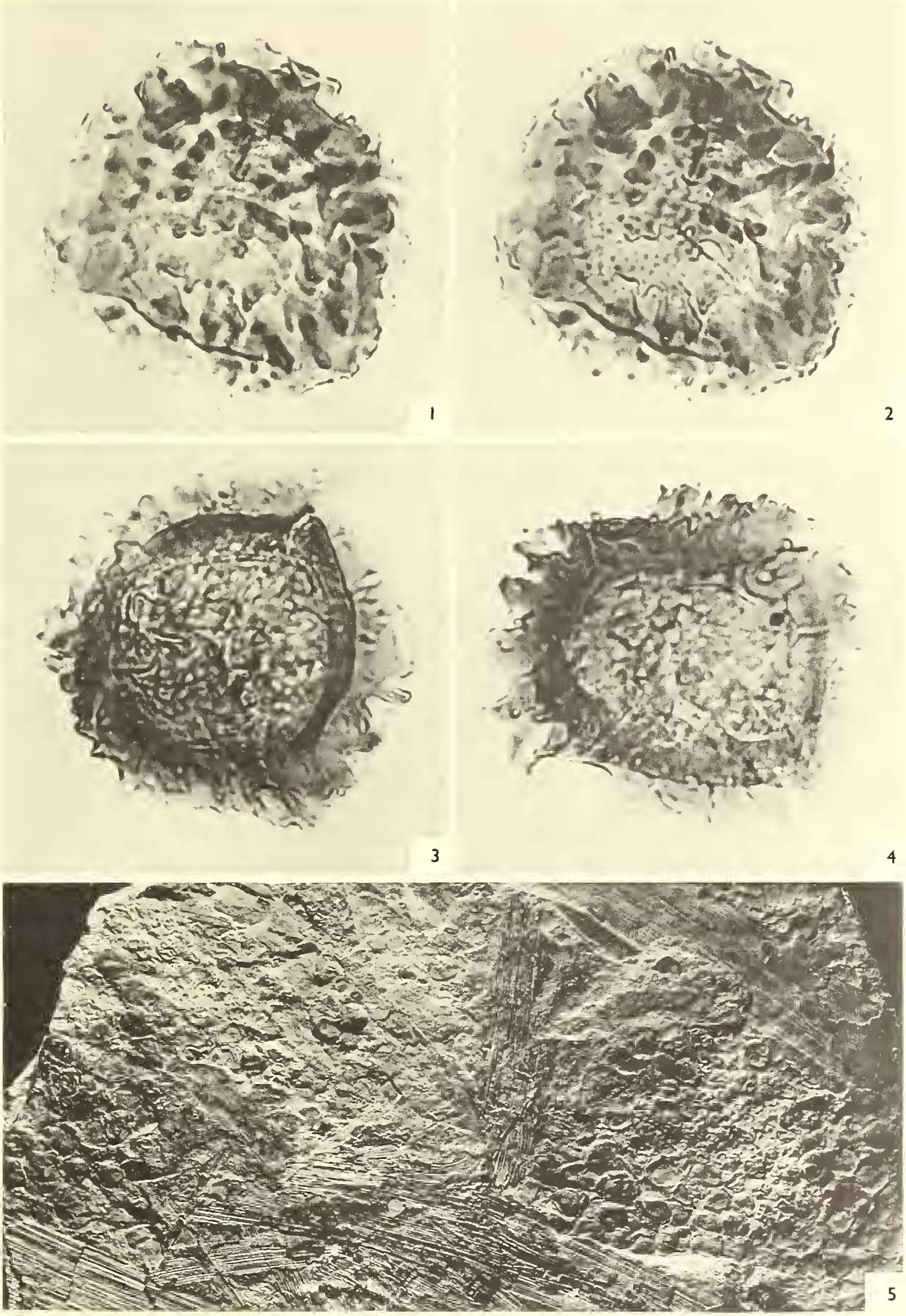
EXPLANATION OF PLATE 10

Figs. 1–4. Microspores from *Sporangiostrobus ohioensis* sp. nov., ×1,000. 1, Spore with distal surface in focus. 2, Proximal surface of the same spore, showing triradiate mark and punctate sculpture (the cristae seen here in the central area are those on the distal face viewed through the proximal face). 3, Spore in median focal plane showing the dark zone surrounding the central area, exaggerated above and right by secondary folding of the wall. 4, An extreme example of irregularity of outline and margin.

Fig. 5. The holotype of *Sporangiostrobus ohioensis*, consisting of two cone segments (probably parts of a single cone), ×1. Compare text-fig. 2. Megaspores can clearly be seen in megasporangia in both parts of the cone. The larger smooth discs are microsporangia.

(Figs. 1–4 are based on single spore mounts all on slide 8134 Ga; fig. 5 is of specimen 8134 G. Palaeobotanical Collection, New York Botanical Garden.)



CHALONER, Carboniferous fructification

of the genus, rather than *S. orzeschensis* as suggested by Andrews (1955). *S. feistmanteli* is also far better known, from Nemejc's investigation, while *S. orzeschensis* is known only from a microspore-bearing cone segment.

2. *S. cordai* (Feistmantel) Nemejc 1931, megaspore-bearing, possibly hermaphrodite; Upper Carboniferous of Czechoslovakia. Although Nemejc does not actually use this combination, he refers (1931, p. 68) to *Sigillariostrobus Cordai* Feistmantel as 'belonging to Bode's type of *Sporangiostrobus*'.

3. *S. orzescheusis* Bode 1928, microspore-bearing; Upper Carboniferous of Orzesche, Silesia, Germany.

4. *S. rugosus* Bode 1928, microspore-bearing; Upper Carboniferous of Orzesche, Silesia, Germany.

5. *S. langfordi* Chaloner 1956, megaspore-bearing; Upper Carboniferous (Pennsylvanian), Illinois, U.S.A.

The nature of the parent plants which bore *Sporangiostrobus* cones is still unknown. Nemejc at one time (1931) urged that some *Lepidodendron* species (e.g. *L. dichotomum*) were likely to be the plants which bore *Sporangiostrobus*; he later (Nemejc 1946) revised this view and said 'The cones called *Sporangiostrobus* are not to be regarded as fructifications of any species of the genera of *Lepidodendron* or of *Lepidophloios*. Their most probable mother plants may be searched among some long leafy lycopodiaceous forms (except the *Sigillariae*) like *Ulodendron* or some other similar types.' The only certain evidence which bears on the question is that the cones are so large that they must presumably have been borne on a correspondingly large (hence ? arborescent) lycopod. The two best-known genera of Carboniferous arborescent lycopods, *Lepidodendron* and *Sigillaria*, are known (in the case of some species at least) to have borne cones which are different from *Sporangiostrobus* in several important respects (Chaloner 1958*a*); to this extent, *Sigillaria* and *Lepidodendron* seem less likely to be the parent plant of *Sporangiostrobus* than other genera (e.g. *Asolanus*) of which the fructification is unknown.

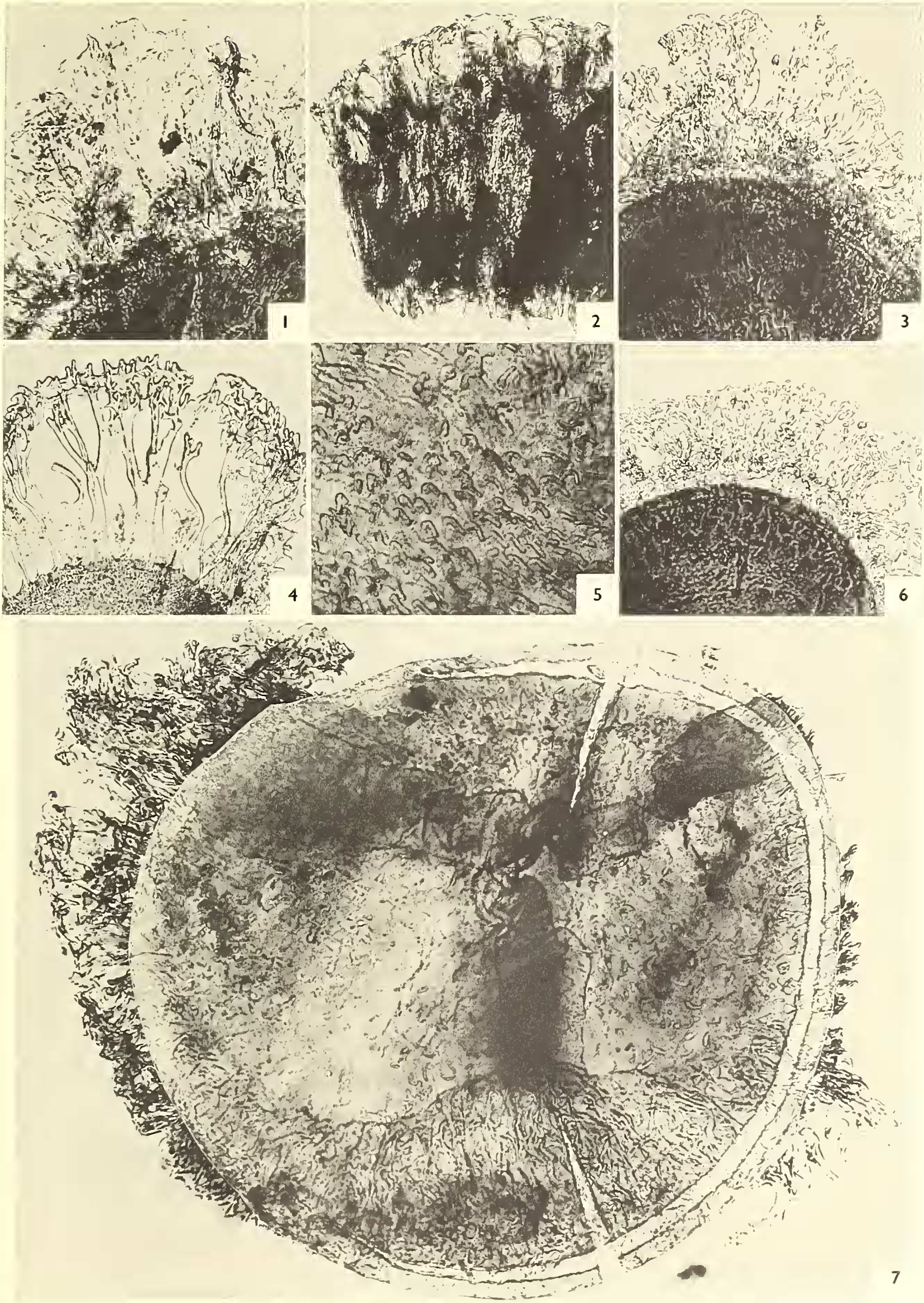
Comparison of Sporangiostrobus ohioensis *with other species.* The characters on which the various *Sporangiostrobus* species may be compared are mainly those of the contained spores. In external features such as size and arrangement of the sporangia, *S. feistmanteli*, *S. langfordi*, and *S. ohioensis* are essentially similar. Of the species containing megaspores, *S. langfordi* was based on a cone segment bearing only megaspores. It is possible that it was, in life, a hermaphrodite cone like *S. ohioensis*, but that in this case only a megasporangiate segment was preserved. Even so, the megaspores of the two species differ in minor details; for example, the more continuous flange in the *S. langfordi* megaspores, which lack the 'spoke and rim' character of the *S. ohioensis* megaspores. On these grounds *S. ohioensis* and *S. langfordi* may be retained as separate species. *S. feistmanteli* is comparable with *S. ohioensis* in being hermaphrodite and having superficially similar mega- and microspores; as the specific character of these cones rests largely on their spore characters, and information on these is rather limited for *S. feistmanteli*, the cone described here has been made the basis of a new species. It is possible that on re-examination of the original specimens, *S. feistmanteli* and *S. ohioensis* may prove to be the same species of hermaphrodite cone, of which *S. langfordi* and *S. rugosus* represent megaspore- and microspore-bearing segments respectively.

Stratigraphic ranges. The threefold correlation of cone, megaspores, and microspores naturally gives added significance to the stratigraphic ranges of the nearest equivalent species of isolated spores. Unfortunately relatively few workers have looked systematically at both megaspores and microspores in the same samples. However, for those instances where this has been done, these ranges may be compared. In Europe generally, combining the records of Potonié and Kremp (1955, 1956*a*) from a number of European sources, *Densosporites solaris* and *D.* (*Cristatisporites*) *indignabundus* taken together have a range throughout the Westphalian B to D, the same range (combined European records) as that of *Superbisporites superbus*, given by those authors. Bhardwaj (1957), examining the Saar coals, recorded in many cases both small spores and megaspores from the same samples, and it is significant in the context of the present work that the microspore genera *Densosporites* and *Cristatisporites* and the megaspore genus *Zonalesporites* all come to an end in the upper part of the Westphalian C. Kosanke (1950) showed that the genus *Densosporites* s.l. (including '*D. indignabundus*') is restricted in Illinois to the Tradewater and Caseyville groups, while Winslow (1959) studying megaspores in the same Illinois coals showed that the zonati section of *Triletes* (zonate megaspores including *Superbisporites*, *Zonalesporites*, and *Rotatisporites*) are restricted to this same range. Smith (1957, p. 360) discussing the significance of the association of *Densosporites* with crassidurite bands in coal refers to 'Densospores and the megaspores of the genus *Superbisporites* always found with them'. A more significant measure of this association is given by the following data kindly supplied by Dr. H. Grebe (personal communication, May 1961). 195 samples from four boreholes in the Westphalian B and C of the Ruhr (both coals and shales being examined) were analysed for both megaspores and miospores. Of these samples, 122 contained densospores (*Densosporites* and/or *Cristatisporites*); 58 contained large zonate megaspores (combined *Zonalesporites* and *Superbisporites*); and of these, 48 contained both large zonate megaspores and densospores. Testing for the significance of the association of these two groups of spores gives a χ^2 value of 14·9; with one degree of freedom, this gives a corresponding value for p of less than 0·1 per cent. This indicates a very strong positive correlation between the occurrence of densospores and the large zonate megaspores in these Ruhr samples. The spore contents of *Sporangiostrobus ohioensis* suggest that this correlation is due at least in part to identity of parent plant rather than just fortuitous (e.g. ecological) association.

EXPLANATION OF PLATE 11

(All figures are $\times 50$ except where otherwise stated, and were photographed by transmitted light).

Figs. 1, 2. Detail of equatorial feature of *Superbisporites superbus*. 1, From Ann Arbor Drift coal (Mich., U.S.A.), prepared by H. H. Bartlett. 2, From the Sub-Babylon coal Fulton County, Illinois, U.S.A. (feature detached from the spore body). Fig. 3, Detail of megaspore of *Sporangiostrobus ohioensis* sp. nov. Fig. 4, Equatorial feature of *Rotatisporites rotatus*, from the Namurian, Ballycastle Coalfield, N. Ireland. Fig. 5, Hairs on the distal face of megaspore of *S. ohioensis*, $\times 80$. Fig. 6, Equatorial feature of *Rotatisporites ramosus* from the Williamston spore coal, Michigan, U.S.A. Fig. 7, Megaspore of *S. ohioensis*, split around part of the margin by compression, and with the equatorial feature damaged. This is a compound photograph made by combining the central body from a negative given a long exposure, with the more transparent equatorial feature from a negative of shorter exposure. (Fig. 1, Slide no. V. 43740; fig. 2, Slide no. V. 43738; fig. 6, Slide no. V. 43739, all in the British Museum, Natural History, London. Figs. 3, 5, 7, Slide no. 8134 Gy, Palaeobotanical Collection, New York Botanical Garden. Fig. 4, Slide no. Mik (C) 245, Geological Survey and Museum, London.)



CHALONER, Carboniferous megaspores